XXVII.—ON THE STRUCTURE AND USES OF THE STOMATA.*

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THE ultimate organization and functions of the Stomata of Plants have long formed the subject of hypothesis and dispute among high authorities in vegetable physiology.

The best informed of the earlier observers regarded them as follicular pouches of the epidermis, through which the aqueous portions of the elaborated sap were exhaled. In his more recent work, it is stated by De Candolle, that they constitute the spaces where the spiral vessels end, and through which the latter obtain their supply of air; and hence has probably originated the title of "breathing holes," under which they are popularly known. By many modern botanists, they are described as definitely organized openings leading into cavities which freely communicate with the spaces between the cells of the parenchyma. There are not wanting others, by whom the *patulous* state of the stomata has been denied, who consider them to be closed by a membrane, described as a continuation of the epidermis, and which from its delicacy and transparency is invisible under ordinary circumstances. The mode adopted by the Rev. Mr. Reade to render evident this pellicle under the microscope, consists in charring the leaf to be examined, between two pieces of glass. Anxious to determine practically the relative merits of these conflicting observations, I submitted the leaves and green parts of several plants to this charring process; and unquestionably succeeded in rendering appreciable, in many instances, the existence of a pellicle over the stomata. But in order to be certain that this membrane was not the result of heat employed in preparing the leaf, of which I had some suspicion, I contrived a modification of the process suggested by the Rev. Mr. Reade. After having determined, by repeated observation, that *some* of the stomata in the spatha of the garden rhubarb *appeared open*, it was immersed in warm water, after which air was gradually forced into the parenchymatous interspaces, under the receiver of an air-pump,—the success of the injection being indicated by the extrication of minute bubbles of air from the inferior surface of the leaf. The escape of the air was evidently made through the stomatal orifices

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—this, at least, is the probable inference—and if admitted, a proof is afforded of the *open* condition of the stomata. The *injected* leaf was then carbonized between plates of glass, and again examined with reference to the condition of the stomata. Surprise was excited when, notwithstanding the proof of the patency, as presented by the escape of the infused air, a pellicle over the stomata, darkened by the charring as in the uninjected leaf, was observed under the microscope. This similarity of result, obtained by processes of experiment essentially different, establishes the correctness of my former suspicion, that the membrane is generated in the preparation of the leaf. Nor is this circumstance difficult of explanation, since in all plants a gummy substance, called by the Germans *Phycomater* or organic mucus, covers the surface and even the cells of the stomata and parenchyma; constituting, according to the more recent observations of Schwann, the materials out of which cells are originally formed. In reference to the stomatal pellicle, therefore, in the lamina of a fully developed leaf, the explanation is most probable which supposes that the air which, always in minute quantities, occupies the intercellular spaces, dilating under the heat of charring, acquires force enough to carry before it a bubble of this mucous substance, the summit of which becomes carbonised when brought into contact with the heated glass. By adhering to the margins of the aperture, it thus presents the appearance of continuity with the surrounding epidermis. In the examination of stomata generally, however, it should be remembered, that in some species of plants this mucous covering assumes the form of a universal cuticle, and by its induration over the stomata forms a distinct unorganised membrane.

After having multiplied to a few additional instances the observations, of which the results are just stated, it became evident that the stomatal organs, even in a limited portion of cuticle, exhibited different characters. By carefully detaching the epidermis from the stem of the *Tradescantia*, the stomata could be distinguished in a perforate condition, without any variation either in the figure or diameter of the orifices. In making, however, a comparative examination of portions of cuticle stripped from the inferior surface of a maturely formed leaf at the base, and from a small expanding bud at the summit of the stalk, differences in the form of the stomatal organs were again recognised. It was not until my examinations had been extended to several other plants, that I associated these varieties with differences in the *age* of the leaf from which the cuticle was taken for inspection. On the young and old leaves of the *Anchusa angustifolia*, and still more strikingly (if the

cuticle, which is dense, be shaved off with a sharp, thin scalpel) on the buds and expanded leaves of the *Ficus elastica*, when contrastively examined, the following distinctive features can be readily determined. Previously charred, the cuticle from the younger leaves will present stomata, which consist of two or more elliptically disposed vesicles, enclosing apparently a membrane, darkened by the charring, which can be distinctly observed to be bisected by a diaphanous line longitudinally traversing the oval space of the stoma. These appearances can likewise be distinguished in the uncharred cuticle, with the difference, however, that the membrane here appears more like flattened cells, studded in their interior with granules of chlorophyll, which impart to the oval space a shaded or dark character; and this latter circumstance explains away the error of the idea which some microscopists have entertained, that the dark appearance is caused by the presence of air in the cavity beneath. In the epidermis of the older leaves, on the contrary, charred or uncharred, unequivocal perforations can be discovered bounded by transparent vesicles. Between these two extremes of the foetal and adult formations, numerous intermediate conditions are presented. The transparent line, which I have satisfied myself to be a fissural aperture between the two apposed, darkened vesicles, with advancing development, acquires greater breadth, until ultimately it assumes the character of an oval orifice. By comparing the stomates on the bases and apices of the leaves of the *Hyacinthus orientalis*, the distinctions here indicated may be conclusively determined. Subsequently to the settlements of these points, my attention was directed to the observations of M. Hugo Mohl* on the development of these organs, in which allusion is made to the views of M. Mirbel.† While no positive statement is made in regard to the persistent condition of the stomata, it may be obviously seen that the account which is here presented, derives confirmation from their labours. These observers conducted their examinations upon the leaves of the *Marchantia polymorpha*, stalks of Gourds, and on the cuticle covering the articulations of *Tygnema*. Although their opinions are somewhat different, they agree upon the principle, that the orifices of these organs result from the graduated separation of the vesicles, which are nothing more than ordinary epidermoid cells, modified into a specific form. These facts, then, obviously point to the general inference, that the normal condition of the stomata is that of complete perforation, and that when the ap-

* Annales des Sciences Naturelles, 1840, p. 222.

† Comptes Rendus, Tom. iii., p. 568.

pearance of an overlying membrane, *without* a central chink, is remarked, its adventitious formation may be inferred.

Whatever may be the difficulty of circumscribing into a definite function, the process of respiration in vegetables, physiologists can no longer doubt the tendency of facts in relation to the use of the stomata. It suggested itself to me, that if some expedient were contrived to suspend the functions of the stomata, a sort of negative or pathological evidence might be obtained in regard to their uses. The most effectual means, after some trials, were found in common varnish. If the *superior* surface of an aquatic leaf, to which it is known the stomata are confined, be well coated with varnish, after the lapse of a few days a distended, unhealthy, and ætiolated state will supervene. Under the conditions of this experiment, it is evident that two important consequences follow :—That, firstly, the process of exhalation is rendered impracticable by the impervious coating, inducing thus an undue retention of water in the Parenchymatous cells; and that, secondly, since the decomponent agency of the light continues, the liberated oxygen is equally retained, and, if the diseased appearance of the leaf be admitted as criterion, proves deleterious to its organism. Time and opportunity have not allowed me to correct and multiply these observations. So far as my acquaintance with botanical literature extends, I am not aware that this mode of experimenting upon the stomata has been anticipated. From various physiological considerations, the accuracy of the analogy cannot be doubted, which makes the stoma to the pneumatic or respiratory system of the plant, what the spiracle is to the tracheal apparatus of the insect. Although the former description of M. De Candolle, that the spiral-vessels communicated by open mouths with the stomatal cavities, has been denied by high authorities in modern phytology, from the experiments of Dutrochet, Dumas* and Dr. Boucherie, it is obvious that the spiral-vessels derive their supply of *atmospheric air* by means of the stomata. In the leaf of the Holly, which, upon maceration, separates into two layers, I have satisfied myself that the spiral-vessels accompany only the excurrent woody fibres, and are therefore confined to the upper lamina of the leaf. A parallel to this arrangement is found in the structure of some insects, in which the tracheal tubes follow *only* the centrifugal currents of blood. In the Holly, therefore, the communication with the stomata at the inferior surface, can only be indirectly through the intercellular passages.

* Comptes Rendus de l'Academie des Sciences, 1840.